RECONSIDERATION OF *OENOTHERA* SUBG. *GAUROPSIS* (ONAGRACEAE)[1]

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ABSTRACT

Oenothera havardii and *O. dissecta,* primarily of northern Mexico, and a third species, *O. canescens,* of the High Plains of the U.S., previously were placed together in subg. *Gauropsis* by P. A. Munz. New data on morphology, cytology, and seed anatomy were gathered to evaluate the relationships of these species to one another and to the remainder of the genus. *Oenothera canescens* is diploid, $n = 7$; *O. dissecta* tetraploid, $n = 14$; and *O. havardii* has both diploid and tetraploid populations. Morphological and anatomical data clearly demonstrate that *Oenothera havardii* is not closely allied with the other species placed in subg. *Gauropsis*. Further, *O. havardii* is not closely related to any other species in the genus, and therefore, it is placed in a new monotypic section, sect. *Paradoxus*. The remaining two species are not closely related, but they do appear to be more closely related to each other than either is to any other species. For this reason, they are here retained in sect. *Gauropsis*. Sect. *Gauropsis* is related to sect. *Hartmannia,* and especially to the white-flowered species, *Oenothera tetraptera* and *O. kunthiana*. The phylogenetic relationships of *O. havardii* are obscure, at best, but it appears to represent a lineage that diverged relatively early in the evolution of the genus. It may have shared a common ancestor with species of sects. *Anogra, Gauropsis, Hartmannia, Kneiffia, Lavauxia,* and *Xylopleurum*.

Oenothera subg. *Gauropsis* has been studied relatively little. Only Munz (1932, 1965) has published taxonomic studies of these plants during the past 50 years. Munz included three species, *Oenothera canescens, O. dissecta,* and *O. havardii,* which had been placed in various segregate genera in the past: *O. canescens* in the monotypic genus *Gaurella* (Small, 1896); *O. canescens* and *O. dissecta* as members of the genus *Megapterium* (Britton, 1894; Small, 1896); and *O. dissecta* and *O. havardii* in the genus *Hartmannia* by Rose (1905). These species were apparently an enigma to Munz, one that was heightened because his study was based on very few specimens, especially of *O. havardii* and *O. dissecta*. He grouped them together in subg. *Gauropsis* partly because they did not fit conveniently into any other of his subgenera. He stated that they shared several features such as bushy habit, ovoid capsules with angled or keeled valves, and seeds in several rows per locule.

These three species do share a bushy to sprawling habit, but it is difficult to ascertain whether this suggests a relationship between them or merely superficial similarity. Ovoid capsules not only occur in these species, but also in several other sections of the genus, some of which differ greatly in other respects. The disposition of the seeds in several irregular rows per locule occurs in *O. canescens* and *O. dissecta,* but not in *O. havardii,* which has seeds in one or two rows per locule. On the other hand, there are numerous

[1] This work was supported by a grant to Peter H. Raven from the U.S. National Science Foundation while I was at the Missouri Botanical Garden. I am grateful to Peter Raven for many helpful discussions, assistance, and for many helpful comments on an earlier draft of the manuscript; Prof. Wilfried Stubbe, Peter Raven, Ching-I Peng, and W. M. Klein for providing unpublished chromosome counts and living material; Mario Sousa for assistance with preparation for fieldwork in Mexico; and A. Michael Powell for providing live plants of *Oenothera havardii* from Texas. I thank Wanling Peng for the excellent illustrations; Susan Mill for careful preparation of the map, and for typing and editing the manuscript; Emily Colletti and Jim Henrich for care of greenhouse material; and the staff of the Missouri Botanical Garden for providing work space and kind assistance. I appreciate the assistance in fieldwork by Lori Brown and Jim Solomon. I would also like to thank the staffs of the following herbaria for the loan of material for this study: A, AC, ALTA, ARIZ, ASC, ASTC, ASU, B, BAYLU, BH, BM, BRY, CAN, CAS, CM, COCO, COL, CS, CU, DAO, DHL, DS, DUKE, E, ENCB, F, FHKSC, G, GH, ID, IDS, ILL, ILLS, ISC, JEPS, KANU, KNOX, KSC, KSP, LA, LL, LSU, LTU, MASS, MEXU, MICH, MIN, MNA, MO, MONT, MONTU, MSC, NA, NCU, ND, NDA, NDG, NEB, NESH, NMC, NY, OKL, OKLA, OS, P, PENN, PH, POM, RM, RSA, SAT, SMU, SRSC, TAES, TEX, TTC, UC, UMO, UNM, US, UT, UTC, VT, WIS, WS, WTS, YU.

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differences between these three species in characters such as flower color, habit, and capsule morphology, and there appear to be few if any characters that clearly link them. For these reasons, it is difficult to maintain subg. *Gauropsis* in its present form.

Recently, a series of modern systematic studies of *Oenothera* have been initiated, typically involving an investigation of crossing relationships, cytology, and examination of variation within and between populations in the field (Dietrich, 1977; Straley, 1977; Raven et al., 1979; Dietrich et al., 1985; Wagner, unpubl. data; Wagner et al., 1985). In 1978 I began study of the species Munz included in subg. *Gauropsis* at the Missouri Botanical Garden. The basic thrust of the study was to gain a better understanding of the relationships of these three distinctive species to one another and to the remainder of the genus, and to provide an expanded taxonomic treatment of them based on extensive field and herbarium study. Munz saw only limited herbarium material and apparently observed only *Oenothera canescens* in the field. This treatment is based on the study of over 500 pressed collections, observations of populations of each species throughout its range, and study of several cultivated strains of each species grown together. Evidence from a genus-wide study of the anatomy and morphology of seeds (Tobe et al., unpubl. data; Wagner, unpubl. data) is also considered here along with the other information.

The information available was considered in the light of three alternative hypotheses: 1) all three species should be placed in monotypic sections, 2) *Oenothera canescens* and *O. dissecta* should be kept in sect. *Gauropsis* with *O. havardii* removed to its own monotypic section, or 3) one or more of these species should be placed with related species in sect. *Hartmannia* sensu lato. These possibilities were evaluated in relation to the narrow sectional concepts of Lewis and Lewis (1955).

Cytology

Cytological observations to determine chromosome number, and in certain strains the meiotic configuration, were made on root-tips or buds from field collections or from greenhouse-grown progeny from field-collected seed. Buds for meiotic chromosome studies were fixed and stored in 1 : 3 acetic acid : absolute ethanol under refrigeration. Prior to staining in 1% acetocarmine buds were hydrolyzed in a mixture of concentrated HCl and 95% ethanol for 20 minutes. Fresh root-tips were prepared for examination with a four hour treatment in 8-hydroxyquinoline and fixed for at least one hour in 1 : 3 acetic acid : absolute ethanol. The root-tips were then hydrolyzed for ca. six minutes in 10% HCl and stained in 2% propionic-carmine.

A total of 11 strains representing all three species have been examined (Table 1), including three unpublished reports provided by Peter Raven and Wilfried Stubbe. The one strain of *Oenothera canescens* examined was diploid, $n = 7$. In contrast, the majority of the counts made for *O. dissecta* and *O. havardii* were tetraploid. *Oenothera dissecta,* sampled throughout its range, appears to be entirely tetraploid, whereas *O. havardii,* also sampled throughout its range, is tetraploid in Arizona and Mexico, but diploid in western Texas. Quadrivalents occur frequently in meiosis in the tetraploids of both *O. dissecta* and *O. havardii,* indicating that the two diploid sets of chromosomes in each of these species would pair at meiotic metaphase I, and suggesting that they might literally be autotetraploids. This fact, in conjunction with the occurrence of diploid plants of *O. havardii* in Texas, suggests that polyploidy has occurred independently in both species. The addition of these two species brings the total number of polyploid or partly polyploid species in *Oenothera* to ten (ca. 8% of the genus), distributed in eight sections. Half of these, like *O. havardii,* include both diploid and tetraploid populations.

Greenhouse Study

The experimental study of *Oenothera canescens, O. dissecta,* and *O. havardii* at the Missouri Botanical Garden has been difficult. Most strains reproduced almost entirely vegetatively by adventitious shoots from lateral roots, especially during stress periods, and all three species were particularly susceptible to fungus in the hot, humid climate of St. Louis. *Oenothera havardii* and *O. canescens* flowered sparsely when grown outside, and *O. dissecta* produced only four flowers during three years of cultivation. The following results must be viewed with these limitations in mind. Strains studied are listed in Table 2. A majority of the flowers produced in all three species were used to test for self-incompatibility by self-pollination. Plants grown from strain (a) of *O. dissecta* were self-compatible, as were those

TABLE 1. Chromosome observations of plants in sects. *Gauropsis* and *Paradoxus*. All specimens deposited at MO.

Species	Locality	Collection	Source or Investigator[a]	Chromosome Observations[b]
sect. *Paradoxus*				
Oenothera havardii				
	Mexico			
	Chihuahua	*Wagner & Brown 3922*	W	$2n = 28$
	Durango	*Wagner & Brown 3935*	W	$5_{IV} + 4_{II}$
	U.S.A.			
	Arizona			
	Cochise Co.	*Wagner 3813*	W	$2n = 28 + 2$–5 b's
	Texas			
	Brewster Co.	*Powell 3901*	W	$2n = 14$; 3 plants
	Presidio Co.	*Powell s.n. in 1982*	W	$2n = 14$
		Powell 2195	P. Raven	$2n = 14$
			W. Stubbe	$2n = 14$
sect. *Gauropsis*				
Oenothera dissecta	Mexico			
	Jalisco	*McVaugh 16984*	P. Raven	$5_{IV} + 4_{II}$
	Zacatecas	*Wagner & Solomon 4224*	W	$2n = 28$
		Wagner & Solomon 4237	W	$2n = 28$
		Wagner & Solomon 4251	W	$2n = 28$; 2 plants
Oenothera canescens	U.S.A.			
	Texas			
	Lubbock Co.	*Raven 19293*	P. Raven	$5_{II} + \odot 4$

[a] Literature source or investigator who made the determination; W = Warren L. Wagner.
[b] ⊙ = ring at meiotic metaphase I or diakinesis; II = bivalent; IV = quadrivalent.

of strains (a) and (b) of *O. canescens*; in contrast, plants of all four strains of *O. havardii* were self-incompatible. Attempts at interspecific hybridization among the species listed in Table 2 uniformly failed.

MORPHOLOGY AND ANATOMY

In this section the characters that are useful in delimiting *Oenothera canescens, O. dissecta,* and *O. havardii* and those that are critical in the evaluation of relationships will be discussed. Careful comparison of a wide array of characters is essential in any attempt to evaluate the relationships of these isolated species to each other and to the rest of the genus.

Habit. All three species begin growth as a rosette, as typical in *Oenothera.* The rosette leaves are normally quickly lost, but in *O. canescens* they are somewhat persistent. Plants of all three species form clumps of sprawling or decumbent stems. In *O. havardii,* and to some extent also in *O. dissecta,* the stems often twine among other grasses and herbs. Plants of *O. canescens* tend to form clumps up to 50 cm across from adventitious shoots from lateral roots. Both *O. havardii* and *O. dissecta* also have the ability to form adventitious shoots, but the above-ground leafy portion dies back during the dry season. When the rains return, numerous new shoots sprout from the roots. Consequently, they do not form clumps. In fact, this is the principal means of reproduction in these two species; both produce few capsules.

Leaves. The three species have rather similar leaves (Figs. 1–7), ranging from lanceolate to linear. In general, the rosette leaves in all three species (e.g., Fig. 7) are larger and have fewer

and more shallow teeth than the cauline leaves. The principal differences between the species are in leaf size and margins. *Oenothera havardii* (Figs. 5, 6) has pinnately lobed to sinuate-dentate leaves 1–5 cm long, whereas *O. dissecta* has mostly irregularly pinnatifid leaves with linear-oblong to linear lobes, the blades 2–8 cm long (Fig. 3) or the lower ones sometimes irregularly pinnately lobed (Fig. 4). *Oenothera canescens* (Figs. 1, 2) has sinuate-denticulate to subentire or rarely serrate margins and blades mostly 0.6–1.5 cm long.

Pubescence. These three species typically have only one hair type, rather than two or three as is common in many other species of *Oenothera.* The terminology here follows that established for *Oenothera* in Wagner et al. (1985). All three species are predominantly strigillose, and the hairs are typically 0.1–0.3 mm long. In *Oenothera dissecta,* the hairs are rarely to 0.4 mm, whereas in *O. canescens* they typically are 0.4–0.6 mm long, or rarely to 0.8 mm. *Oenothera dissecta* also is occasionally sparingly hirsute only on the margins and veins of the leaves. The hairs of this pubescence type are mostly straight with slightly broadened bases and are 0.6–1.5 mm long. Both the strigillose and hirsute types are similar in morphology and length to those same types in many other sections of the genus.

Buds. The buds of all three species are erect. *Oenothera havardii* and *O. canescens* both lack free sepal tips, while in *O. canescens* they may occasionally be present and are 0.2–0.3 mm long. In contrast, *O. dissecta* has conspicuous free sepal tips 1–6 mm long.

The buds of all three species split along one suture and are reflexed to one side as a unit, although those of *O. canescens* occasionally split along two sutures and the sepals are reflexed in pairs. Similar patterns of anthesis are common in several sections of the genus. The buds of *O. havardii* are unique in that they are often somewhat twisted.

Flowers. Both *Oenothera havardii* and *O. dissecta* have one to occasionally several flowers opening per day near sunset, the common flowering pattern for the genus, especially for the hawkmoth-pollinated species. *Oenothera havardii* is pollinated by *Hyles lineata* (Fabricius) according to Gregory (1963, 1964). *Oenothera dissecta* is also visited by hawkmoths, based on observations of an unidentified hawkmoth visiting flowers of this species in Zacatecas, Mexico (*Wagner & Solomon 4217*).

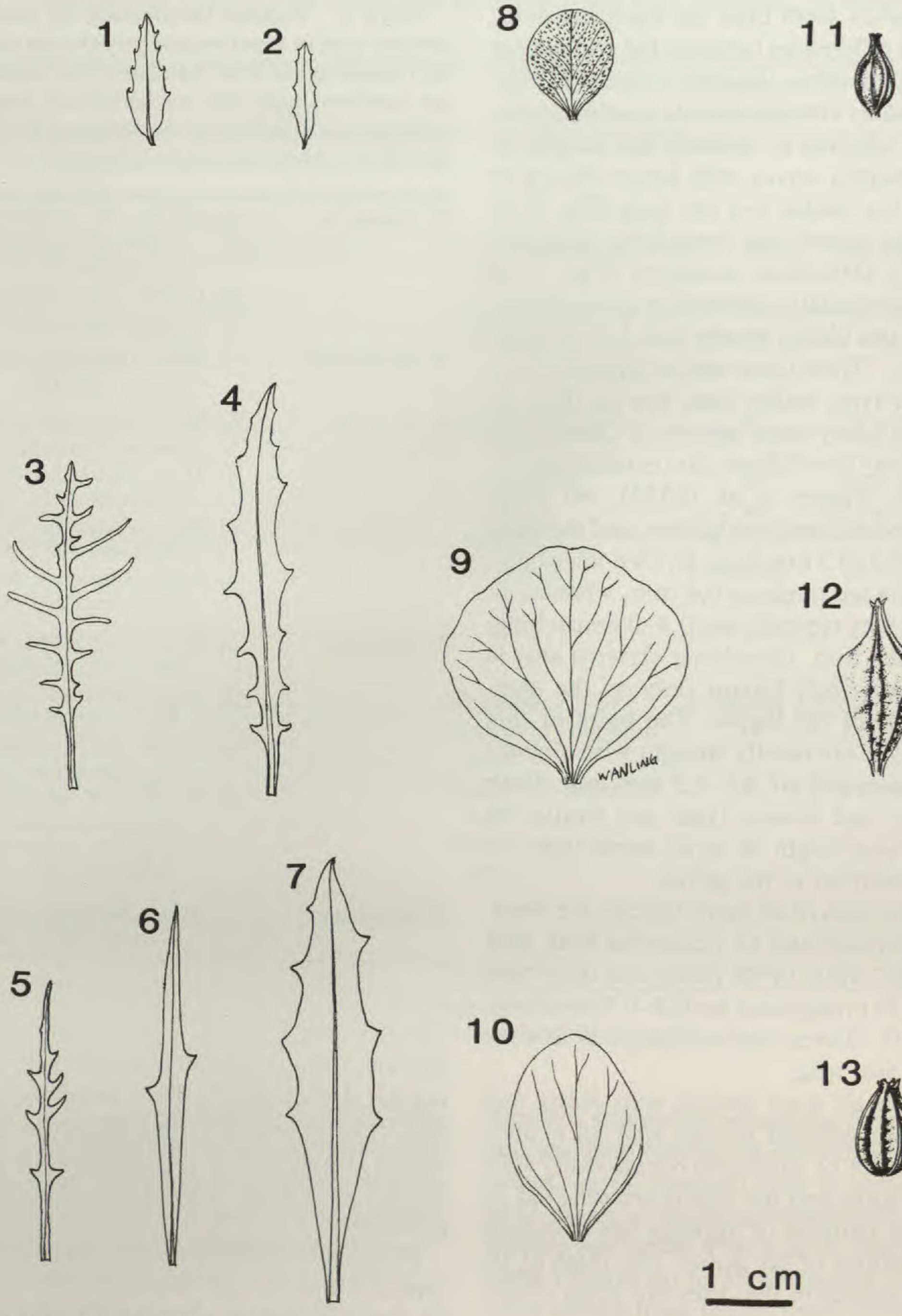
In contrast to this widespread pattern, *Oenothera canescens* typically has many flowers opening per day at sunset. This specialization is perhaps related to a shift to pollination by noctuid moths (Raven, pers. comm.), which visit these flowers in greater abundance than hawkmoth pollinators.

Floral tube length is somewhat variable as is typical for many species of *Oenothera.* Those of *O. havardii* and *O. dissecta* fall into the typical range for species pollinated by short-tongued hawkmoths such as *Hyles*; those of *O. havardii* are (3.7–)4.5–6(–6.5) cm long; whereas those of *O. dissecta* are somewhat shorter, (2.6–)3.5–4.2 cm long. The floral tubes of *O. canescens* are considerably shorter, (0.8–)1–1.5(–1.7) cm long, which presumably is related to visitation by the shorter-tongued noctuid moths.

Each of the three species has petals of a different color. *Oenothera havardii* has lemon yellow petals, which is the presumed ancestral color for the genus. In contrast, *O. dissecta* has white

TABLE 2. Voucher information for strains of *Oenothera* used in experimental greenhouse study. Numbers following collector numbers refer to garden planting numbers, used also on herbarium vouchers. All vouchers are deposited at the Missouri Botanical Garden (MO), unless otherwise indicated.

O. canescens:	a) U.S.A., TX, Lubbock Co., *Raven 19293* (seeds from *W. Stubbe 65-135*); *M1209.*
	b) U.S.A., CO, Cheyenne Co., *Wagner 3691*; CO-3.
O. deserticola:	Mex., Durango, *Breedlove 44134*; *M2088.*
O. dissecta:	a) Mex., Zacatecas, *Wagner & Brown 3980*; MEX-5.
	b) Mex., Zacatecas, *Wagner & Solomon 4224*; MEX-7A.
	c) Mex., Zacatecas, *Wagner & Solomon 4237*; MEX-8.
	d) Mex., Zacatecas, *Wagner & Solomon 4251*; MEX-9.
O. havardii:	a) Mex., Chihuahua, *Wagner & Brown 3922*; MEX-1.
	b) Mex., Durango, *Wagner & Brown 3935*; MEX-2.
	c) U.S.A., AZ, Cochise Co., *Wagner 3813*; AZ-3.
	d) U.S.A., TX, Brewster Co., seeds from *Stubbe 67-381* originally from *Powell 2195*; M1208.
O. kunthiana:	Mex., Zacatecas, *Wagner & Solomon 4226*; MEX-7b.



FIGURES 1–13. Leaves, petals and capsules of *Oenothera canescens, O. dissecta,* and *O. havardii.* 1–7. Leaves.—1, 2, *O. canescens,* Sedgwick Co., Kansas, *Stephens 55690* (KANU).—3, 4. *O. dissecta,* Mexico, *Schumann 531* (GH).—5–7. Two cauline leaves and one basal (7) of *O. havardii,* Chihuahua, Mexico, *Wagner & Brown 3922* (MO). 8–10. Petals.—8. *O. canescens, Stephens 55690.*—9. *O. dissecta, Schumann 531.*—10. *O. havardii, Wagner & Brown 3922.* 11–13. Capsules.—11. *O. canescens,* Cheyenne Co., Colorado, *Wagner 3691* (MO).—12. *O. dissecta,* San Luis Potosí, Mexico, *Parry & Palmer 249* (BM).—13. *O. havardii,* Chihuahua, Mexico, *Pringle 1146* (VT).

petals, similar to those of the presumably related species, *O. tetraptera* and *O. kunthiana* (sect. *Hartmannia*). Apparently white petals have also evolved independently in the common ancestor of sect. *Pachylophus* (five species), in *O. muelleri* Munz and *O. tubifera* Sér. of an undescribed related section, in both species of sect. *Kleinia,* and in *O. centauriifolia* Spach and *O. acaulis* Cav. of sect. *Lavauxia. Oenothera canescens* is unique in having petals that are pink or white and

streaked or flecked with red, a pattern possibly related to the shift in pollinators in this species. The petals of both *O. dissecta* and *O. canescens* are obovate, although those of *O. dissecta* are broadly so, sometimes nearly orbicular. Those of *O. dissecta* are rather typical in size for the genus, (1.5–)2–4 cm long, whereas those of *O. canescens* are rather smaller, (0.8–)1–1.7 cm long. In contrast, the petals of *O. havardii* are elliptic to occasionally oblanceolate, a shape shared only with several species of sect. *Oenothera* subsect. *Raimannia*. This shape appears to have evolved independently in these two groups. The petals of *O. havardii* are (1.8–)2.1–3(–3.2) cm long.

The red anthers of *Oenothera havardii* are unique in the genus. It should be noted, however, that those of *O. canescens* often have a red longitudinal stripe. With these exceptions, no other species of *Oenothera* is known to have any red in its anthers.

Capsules. Capsules in this group, as is typical for the genus, provide good diagnostic characters for identification and analysis of relationships. Within sections there is usually a high degree of similarity in the capsule features among the species. However, the capsules of these three species differ in texture, shape, ornamentation of the margins of the valves, apex, and degree of dehiscence.

Both *Oenothera havardii* and *O. dissecta* produce relatively few capsules, and seem to reproduce primarily by vegetative means. Although *O. canescens* also reproduces well vegetatively, it also produces large numbers of capsules.

The capsule features of *Oenothera canescens* and *O. havardii* are clearly specialized and unique in the genus. The capsules of *O. havardii* are extremely hard and woody in texture at maturity, and have a prominent median ridge on each valve. They are oblong-ovoid to ovoid, 8–13(–16) mm long, have short, blunt sterile beaks 2–3 mm long, and sharply angled valves. At maturity they are tardily dehiscent for about ⅓ the length of the capsule. *Oenothera canescens* produces capsules that are also very hard at maturity, ovoid, (7–)9–12(–14) mm long, and abruptly constricted to a conspicuous sterile beak mostly (2–)3–4.5 mm long. The margins of the valves have narrow wings 0.8–1.5 mm wide running the entire length of the capsule. At maturity they are indehiscent, a feature that is unique in the genus and is most closely approached by *O. havardii.*

In contrast, the capsules of *Oenothera dissecta* are hard and leathery rather than woody. They are ovoid to narrowly ovoid, (9–)13–20 mm long, and abruptly constricted to a sterile beak 2–6 mm long. The valves have a median ridge, although it is not as conspicuous as that in *O. havardii,* and the margins of the valves have triangular wings 2–2.5 mm wide that extend the length of the capsule. These capsule features of *O. dissecta* are rather similar to those of the capsules of *O. tetraptera* and *O. kunthiana* in sect. *Hartmannia. Oenothera dissecta* further shares with the species of sects. *Hartmannia* and *Kneiffia* capsules that dehisce ca. ⅓ their length and have a sterile, basal portion that is pedicel-like. This stipe is 1–4 mm long in *O. dissecta,* whereas it is much longer in species of sects. *Hartmannia* and *Kneiffia.*

Seeds. Seed features have long been employed as a principal consideration in the delimitation of infrageneric groupings in *Oenothera* (Spach, 1835a, 1835b; Raimann, 1893; Munz, 1965). In his summary work on the Onagraceae for "North American Flora," Munz (1965) distinguished his subgenera of *Oenothera* largely on seed and capsule features. Therefore, it was critical to examine in depth the external and internal features of the seeds of *Oenothera havardii, O. dissecta,* and *O. canescens* in order to evaluate their proper placement and relationship to one another. Comparison of the gross features of the seeds of these species is summarized in Table 3. *Oenothera havardii* clearly is the most distinctive of the three species based on its seed characters. Both seed shape and the nonpersistence of the seeds on the placenta at maturity, however, are shared with *O. canescens.* In all other features the seeds of *O. dissecta* and *O. canescens* are essentially identical. Moreover, most of these characters are shared not only between these two species but also with the species of sects. *Hartmannia* and *Kneiffia.*

Table 4 summarizes anatomical features of the testa of these species based on a recent genus-wide study of the anatomical features of seeds (Tobe et al., unpubl. data). As with the external seed characters, the anatomical features of *Oenothera havardii* are clearly distinctive. Likewise, *O. dissecta* and *O. canescens* are virtually identical in their structure of the testa. They only differ in that the exotesta is much thicker in *O. canescens.* In fact, the exotestal cell thickness of *O. canescens* is the greatest in the genus. In summary, comparison of the seed features of these species clearly demonstrates that *Oenothera havardii* is different than the other two species and

TABLE 3. Comparison of seed features of *O. havardii, O. dissecta,* and *O. canescens.*

Seeds	*O. havardii*	*O. dissecta*	*O. canescens*
# rows/locule	1–2	indefinite rows, reduced to one at maturity	2–4
#/capsule	30–60	100–130?	50–100
Shape	asymmetrically cuneiform to rhombic, angled	ovoid, obscurely angled	asymmetrically cuneiform, angled
Color	yellowish green with purple spots to purplish brown	light brown	light brown to brown, dark spot at distal end and micropyle
Size (mm)	2–2.5(–3.3) by 1.2–1.5	1.5 by 0.6–0.8	1.2–1.5 by 0.4–0.5
Surface	distal wing, raised ridge, beaded	smooth and glossy, obscurely reticulate	smooth and glossy, obscurely reticulate
Attachment to placenta	readily detaches	persistent	readily detaches

that *O. dissecta* and *O. canescens* share nearly all features, differing only modally in others.

DISCUSSION

The morphological and anatomical data gathered in this study clearly demonstrate that *Oenothera havardii* is not closely allied with either *O. dissecta* or *O. canescens,* and that it should not be included in the same section with them. In fact, it is not closely related to any other species in the genus, and therefore it is placed here in a new monotypic section, sect. *Paradoxus,* described below. *Oenothera havardii* possesses a number of unique derived characters including red anthers, twisted buds, and distinctively angled capsules, each valve with a prominent median ridge. Closely related groups of species in *Oenothera* (i.e., species of a single section) generally share similar capsule characters, and the fact that *O. havardii* has capsules unique for the genus argues for giving it sectional status. In further support of this, *O. havardii* possesses certain characters that in combination set it apart from other species of the genus, and especially from *O. canescens* and *O. dissecta.* These characters include the elliptic to oblanceolate yellow petals; seeds in 1–2 rows per locule; seed shape, size, and color; and mesotesta 2–5 cells thick, with sclerotic pitted walls and the seed surface with a beaded appearance. Retained primitive features of *O. havardii* include yellow petals; hawkmoth pollination; seeds that readily detach from the placenta; mesotesta 2–5 cell layers in thickness, the cells sclerotic and pitted; and capsules that dehisce ca. ⅓ their length.

TABLE 4. Anatomical features of the testa of *O. havardii, O. dissecta,* and *O. canescens.*

	O. havardii	*O. dissecta*	*O. canescens*
Endotesta			
Thickness (μm)	10.6–12.7	5.3–6.3	4.2–5.3
Cell shape	radially flattened	radially flattened	radially flattened
Cell-wall thickenings	inner wall	inner wall	inner wall
Mesotesta			
Thickness (cell-layers)	2–5	0	0
Cell type	sclerotic, pitted	crushed	crushed
Exotesta			
Thickness (μm)	67.6–99.3	46.5–59.2	74–152
Cell shape	radially elongated, papilla-like	radially elongated, pillar-like	radially elongated, pillar-like

Certain characters that *Oenothera havardii* shares with other species of the genus appear to represent convergent evolution. The leaf size and lobing pattern of *O. havardii* is very similar to that of *O. dissecta.* Many species in the genus, however, have the same basic oblanceolate leaf shape, coupled with toothed or irregularly pinnatifid leaves. The overall similarities of these two species, including the reduction of leaf size, could merely be the result of convergence related to their occurrence in xeric desert habitats. Elliptic to oblanceolate petals, another derived feature, is also shared with several species of sect. *Oenothera* subsect. *Raimannia,* such as *O. rhombipetala* Nutt. ex Torrey & A. Gray. It appears very likely that this shape has evolved independently in both groups, since they have little else in common.

The seeds of *Oenothera havardii* are similar in a number of ways to those of species of sect. *Lavauxia.* The cuneiform seeds of *O. havardii* with a raised ridge, small distal wing, and beaded surface are strikingly similar to the seeds of species of sect. *Lavauxia,* especially the North American members. Seed size is also similar. Moreover, both *O. havardii* and species of sect. *Lavauxia* share similar exotesta cell shape and have thickenings only on the inner wall of the endotesta (Tobe et al., unpubl. data). This type of endotestal cell-wall thickening, however, is found in a large number of species in the genus distributed in several sections. The unique similarities between the seeds of *O. havardii* and those of sect. *Lavauxia* thus are restricted to their size and external morphology. Because of their exposure to the environment, external features of seeds are presumably much more subject to adaptive change than are the internal ones. Therefore, it is difficult to suggest any close relationship between sect. *Lavauxia* and *O. havardii* since they differ in most respects except in the seed features listed above. On the other hand, the anatomical seed features of *O. havardii,* including thin endotesta, the cells radially flattened, with only the inner walls thickened, and greatly enlarged exotestal cells, clearly ally it with that part of the genus including sects. *Anogra, Gauropsis, Hartmannia, Kneiffia, Lavauxia,* and *Xylopleurum* (Tobe et al., unpubl. data).

The remaining two species, *Oenothera canescens* and *O. dissecta,* are not particularly closely related, yet they appear to be more closely related to each other than either is to any other species. They are related to the same group of sections listed above for *Oenothera havardii,* although they are more closely related to them than *O. havardii.* Furthermore, they are most closely related to sects. *Hartmannia, Kneiffia,* and *Xylopleurum,* based on a number of common characters including winged capsules, seeds clustered in each locule, and similar seed size. *Oenothera dissecta* shares even more characters with these sections, including seeds persistent on the placenta, similar capsule shape and capsule wings, and a sterile, basal part of the capsule only 1–4 mm long, which is typically much longer in the other sections. *Oenothera dissecta* further shares white petals with *O. tetraptera* Cav. and *O. kunthiana* (Spach) Munz of sect. *Hartmannia.* It also has suborbicular to elliptic, glabrous cotyledons that are very similar to those of *O. kunthiana* and *O. rosea* L'Hér. ex Ait. of the same section. The full distribution of this cotyledon type, however, is not presently known. These characters appear to be derived ones and suggest a shared common ancestor between sects. *Gauropsis, Hartmannia, Kneiffia,* and *Xylopleurum.* Sect. *Gauropsis* probably is related most closely to *O. tetraptera* and *O. kunthiana.* This relationship has been suggested in the past when Rose (1905) included *O. dissecta* in sect. *Hartmannia.*

Although they are related to species of sect. *Hartmannia, Oenothera dissecta* and *O. canescens* are clearly specialized and therefore should be placed in an adjacent section. To include them in sect. *Hartmannia* would make this section much more heterogeneous than it is at present and more so than many other sections of the genus. The principal unique derived features of *O. dissecta* and *O. canescens* are the specialized sprawling habit and seeds with pillar-like exotestal cells. Vegetative reproduction by adventitious shoots from lateral roots also distinguishes these two species from sect. *Hartmannia,* although it is probably a retained primitive feature. Both species are individually specialized in a number of ways that set them apart from other members of the genus, but especially from sect. *Hartmannia. Oenothera dissecta* appears to be entirely tetraploid and makes only fleeting appearances above ground, spending most of the dry parts of the year underground as rootstocks. This latter specialization is also shared to some degree with *O. havardii,* but appears to have been independently derived in each. Related to this extensive vegetative growth is the very low seed production in *Oenothera dissecta. Oenothera canescens* is even more specialized. Its nut-like, in-

dehiscent capsules are unique in the genus. It also has made a major shift in its breeding system to pollination by noctuid moths. Presumably related to this pollinator shift was the increase in the number of flowers, petal color change, and great reduction in floral tube length. In summary, *O. dissecta* and *O. canescens* do not fit well into any other section of the genus because they have certain shared and unique specializations as well as similar retained primitive features. They are retained together here in sect. *Gauropsis,* which appears to be most closely allied to sect. *Hartmannia.* This is most evident in the similarity of *O. dissecta* to *O. tetraptera* and *O. kunthiana.*

SYSTEMATIC TREATMENT

KEY TO THE SECTIONS OF *GAUROPSIS* AND *PARADOXUS*

1. Petals yellow, elliptic to oblanceolate; anthers entirely red; capsules angled, never winged, each valve with a prominent median ridge; seed surface beaded, dull; self-incompatible ..... I. sect. *Paradoxus*

1′. Petals pink, flecked with red, or completely white, obovate to broadly obovate or nearly orbicular; anthers yellow or sometimes with a red stripe; capsules narrowly winged, the wings 1–2.5 mm wide, each valve with a low median ridge or ridge absent; seed surface obscurely reticulate, appearing finely granular, glossy; self-compatible ..... II. sect. *Gauropsis*

I. **Oenothera** L. sect. **Paradoxus** W. L. Wagner, sect. nov. TYPE: *O. havardii* S. Wats.

Oenothera subg. *Gauropsis* sensu Munz, Amer. J. Bot. 19: 766. 1932, pro parte. N. Amer. Fl., Ser. 2, 5: 93. 1965, pro parte.

Herbae foliosae compactae ad decumbentes, propagatione asexuali per surculos adventitiae e radicibus effusis, caulibus aliquando ad nodos radicantibus. Gemmae saepe tortae, apicibus sepalorum cohaerentibus. Petala citrina, elliptica vel oblanceolata. Antherae rubrae. Capsula durissima, quadrangularia, valvula quoque crista mediana prominente. Semina grosse papillosa, in loculo quoque uni- vel biseriata, seriebus seminorum superpositis.

Leafy, compact to sprawling perennial herbs spreading by adventitious shoots from lateral roots, stems branched or simple, weakly erect becoming decumbent, often twining among vegetation, sometimes rooting at the nodes. Leaves irregularly pinnately lobed to sinuate-toothed or dentate. Buds erect, the apex long-acuminate, often twisted, sepal tips coherent. Petals lemon yellow, fading orangish red, drying reddish purple, elliptic to oblanceolate. Sepals splitting along one suture and reflexed as a unit to one side. Anthers red. Capsules few, very hard, 8–15 mm long, 4-angled and with a prominent median ridge on each valve, tardily dehiscent for ca. ⅓ capsule length. Seeds in 1 row or 2 overlapping rows in each locule, irregularly angled, the surface beaded. Self-incompatible, $n = 7, 14$.

The sectional name, *Paradoxus,* refers to the obscure relationship of *Oenothera havardii* to the other species of the genus.

1. Oenothera havardii S. Wats., Proc. Amer. Acad. Arts 20: 366. 1885. TYPE: Texas. Presidio Co.: Prairies near Marfa, 1,430 m, July 1883, *Havard 122* (lectotype, GH, photo MO; isolectotypes, CU, US; Munz, Amer. J. Bot. 19: 768. 1932). *Hartmannia havardii* (S. Wats.) Rose, Contr. U.S. Natl. Herb. 8: 328. 1905.

Hartmannia palmeri Rose, Contr. U.S. Natl. Herb. 8: 329. 1905. TYPE: Mexico. Durango: near Santiago Papasquiaro [25°03′N, 105°25′W, 1,900 m], Apr. and Aug. 1896, *Palmer 45* (holotype, US-304795, photo MO; isotypes, GH, UC).

Leafy, compact to sprawling perennial herbs, often producing adventitious shoots from spreading lateral roots, stems 5–25(–70) cm long, usually many-branched, sometimes simple, weakly erect becoming decumbent, often twining among vegetation, sometimes rooting at the nodes, canescent-strigillose, the hairs 0.1–0.3 mm long. Stem leaves linear-lanceolate to linear, 1–5 cm long, 2–8 mm wide, pinnately-lobed to sinuate-dentate, the lobes widely spaced, strigillose, sometimes more densely so along the margins, occasionally subglabrous; rosette leaves oblanceolate, few toothed, generally quickly deciduous, 2–5 cm long, 5–15 mm wide; petioles on both types 0–6 mm long. Buds erect, oblong, the apex long-acuminate, often twisted, sepal tips coherent. Flowers 1–few opening per day near sunset. Ovary canescent-strigillose, (7–)9–13 mm long, sessile. Floral tube (3.7–)4.5–6(–6.5) cm long, flaring to 3.6–4.1 mm at the mouth, densely strigillose, glabrous within. Sepals splitting along one suture and reflexed to one side as a unit at anthesis, (1.6–)1.8–2.6(–3) cm long, 1.5–2.3 mm wide, canescent-strigillose, the margins with a conspicuous reddish purple stripe. Petals lemon yellow, fading orangish red, drying reddish purple, elliptic to occasionally oblanceolate, (1.8–)2.1–3(–3.2) cm long, (0.9–)1.2–1.5(–1.8) cm wide. Staminal filaments yellow, 15–18(–22) mm

FIGURE 14. Distributions of *Oenothera canescens* (stars), *O. dissecta* (dots), and *O. havardii* (open triangles).

long. Anthers red, 6–13 mm long. Style (5.5–) 6.5–8.6(–9.4) cm long; stigma lobes red, (2–)3.5–5 mm long, well elevated above the anthers at anthesis. Capsules few, very hard at maturity, oblong-ovoid to ovoid, 8–13(–16) mm long, 3–4 mm diam. tapering to a short sterile beak 2–3 mm long, with free tips 1–2 mm long, the base truncate and slightly asymmetrical, the valves with a prominent broad median ridge, the margins of the valves sharply angled, tardily dehiscent about ⅓ the capsule length. Seeds ca. 30–60 per capsule arranged in 1 or 2 partially overlapping rows per locule, asymmetrically cuneiform to rhombic, often rather irregular (due to compression from packing arrangement), irregularly angled, yellowish green with scattered purple spots to sometimes purplish brown, 2–2.5 (–3.3) mm long, 1.2–1.5 mm wide, sometimes with a small wing at the distal end or a raised ridge along one longitudinal margin, the surface

minutely beaded. Self-incompatible. Gametic chromosome number, $n = 7, 14$.

Distribution. Locally common in depressions, seasonally wet flats, stream banks or margins of irrigated fields, sandy or clay soils, often growing among tufted grasses like *Sporobolus wrightii* Scribn., primarily in the Chihuahuan desert from Marfa (Presidio Co.) and Alpine (Brewster Co.), Texas, Cochise Co., Arizona, south to F. I. Madero, southeastern Durango, Mexico and Juan Aldana, Zacatecas, Mexico, 1,300–2,000 m. Flowering from April to October. Figure 14.

Additional specimens examined. MEXICO. CHIHUAHUA: 5 mi. S of [Rancho los] Gallegos along Hwy. 45, *Breedlove 15732* (DS); 10 mi. S of Montezuma on Hwy. 45, *Dwyer 14157* (MO); 5 mi. E of Allende turnoff on Hwy. 159 from Parral to Camargo, *Freytag & Baxter M64* (MO); 21.2 mi. SW of El Morrion, *Lehto & Broome L22870* (ASU, MO); S of cd. Guerrero, ca. 28°33′N, 107°30′W, *McGill et al. 8363* (ASU); Basuchil, 28°30′N, 107°24′W, *Mexia 2544* (F, GH, MICH, MO, NY, PH, POM, UC, US); vic. of Aldama, 28°30′N, 106°34′W, *Palmer 252* (GH, NY, US); Valle del Rosario, 27°19′N, 106°18′W, *Pennington 367* (TEX); Chihuahua, 28°38′N, 106°05′W, 1887, *Pringle s.n.* (MEXU); near Chihuahua, near 28°38′N, 106°05′W, *Pringle 1146* (GH, VT); 15 km S of Escobillas, near 28°49′N, 104°06′W, *Stewart 2360* (GH); 5 mi. E of cd. Jiménez, near 27°08′N, 104°54′W, *Wagner & Brown 3922* (MO), *White 2137* (MICH). DURANGO: on rd. to Juan Aldama, near 24°19′N, 103°21′W, *Moldenke 1591* (DS); Tepehuanes, 25°21′N, 105°44′W, *Palmer 301* (F, GH, MO, NY, UC, US); 5.2 mi. N of Guadalupe Victoria along Hwy. 40, near 24°27′N, 104°07′W, *Wagner & Brown 3935* (MO); 1.7 mi. NE of F. I. Madero, 24°23′N, 104°19′W, *Wagner & Solomon 4318,* pro parte (MO), vic. of cd. [Guadalupe] Victoria, 34–38 mi. NE of Durango, 24°27′N, 104°07′W, *Waterfall & Wallis 13348* (ISC, OKL, RSA, SMU). SONORA: 0.5 mi. S of Agua Prieta, rd. to Franteras, ca. 31°18′N, 109°34′W, *White 3856* (MICH). UNITED STATES. ARIZONA: Cochise Co., along U.S. Hwy. 80 ca. 3.5 mi. NE of Apache, 1962, *Hespenheide s.n.* (DUKE), *Wagner 3813* (MO); Elfrida, near Douglas, 1957, *Jones s.n.* (RSA). TEXAS: Brewster Co., Alpine, golf course, *Sperry T1332* (TAES, US); Presidio Co., Marfa, 1936, *Hinckley s.n.* (SRSC), *Hinckley 657* (BH, F, GH, NY, SMU), *Hinckley 707* (ARIZ, F, NY), *Hinckley 3472* (BH, CS, NY, RM, RSA, SMU, SRSC 2 sheets, US), *Hinckley 3477* (NY), *Hinckley 3504* (SRSC), 1926, *Orcutt s.n.* (POM, US), *Warnock 14152* (SRSC); Pecos Co., near Leon Spring, near Fort Stockton, 1851, *Wright s.n.* (GH); without further locality, *Smith s.n.* (NY).

Oenothera havardii sometimes occurs in habitats similar to those of *O. dissecta,* and at the southern end of its range, northeast of F. I. Madero, Durango, Mexico (*Wagner & Solomon 4318*), it grows together with it. They coexist here without any signs of hybridization.

II. Oenothera L. sect. **Gauropsis** (Torrey & Frém.) W. L. Wagner, comb. & stat. nov. *Oenothera* L. sect. *Euoenothera* (Torrey & A. Gray) Torrey & Frém. subsect. *Gauropsis* Torrey & Frém. in Frém., Rep. Exped. Rocky Mts. 315. 1845. TYPE: *O. canescens* Torrey & Frém. *Gauropsis* (Torrey & Frém.) Cockerell, Bot. Gaz. (Crawfordsville) 30: 351. 1900, non Presl, Epimel. Bot. 219. 1851 [1849].

Gaurella Small, Bull. Torrey Bot. Club 23: 183. 1896. TYPE: *G. guttulata* (Geyer ex Hook.) Small, nom. illeg. = *Oenothera canescens* Torrey & Frém.

Leafy, bushy to sprawling or compact perennial herbs, spreading by adventitious shoots from lateral roots, stems simple to branched, decumbent to ascending. Leaves lanceolate to linear-lanceolate in outline, strigillose, rarely also sparsely hirsute, basal leaves often oblanceolate, petioles 0–1.5 cm long. Buds erect, with or without free sepal tips. Petals pink and streaked or flecked with red, to white, fading purple to pink, drying purple. Capsules ovoid, constricted to a sterile beak, the valves with narrow wings 1–2.5 mm wide. Seeds in 2–4 irregular rows (or in *O. dissecta* 1 row at maturity by abortion), asymmetrically cuneiform to ovoid or oblanceoloid, angled, glossy, obscurely reticulate, appearing finely granular. Self-compatible. Gametic chromosome numbers, $n = 7, 14$.

KEY TO THE SPECIES OF SECT. *GAUROPSIS*

1. Petals white, fading pink, drying purple, (15–)20–40 mm long; leaves 20–80 mm long, irregularly pinnatifid, the basal ones sometimes merely dentate; capsules (9–)13–20 mm long, dehiscing ca. ⅓ the capsule length; capsule wings 2–2.5 mm wide; Mexico ..... 2. *O. dissecta*

1′. Petals pink flecked with red, fading and drying bright purple, (8–)10–17 mm long; leaves (3–)6–15(–25) mm long, sinuate-denticulate to subentire; capsules (7–)9–12(–14) mm long, indehiscent; capsule wings 0.8–1.5 mm wide; High Plains, U.S.A. ..... 3. *O. canescens*

2. Oenothera dissecta A. Gray ex S. Wats., Proc. Amer. Acad. Arts 17: 357. 1882. TYPE: Mexico. San Luis Potosí: sandy localities near San Luis Potosí [1,850 m], 1876, *Schaffner 168* (lectotype, GH, photo MO; isolectotype, PH; Munz, Amer. J. Bot. 19: 767.

1932). *Megapterium dissectum* (A. Gray ex S. Wats.) Small, Bull. Torrey Bot. Club 23: 184. 1896. *Hartmannia dissecta* (A. Gray ex S. Wats.) Rose, Contr. U.S. Natl. Herb. 8: 328. 1905.

Leafy, compact to sprawling perennial herbs, producing adventitious shoots from spreading lateral roots, stems simple to branched, 0.2–30 (–80) cm long, weakly erect becoming decumbent, older stems woody, strigillose, the hairs 0.1–0.3(–0.4) mm long. Stem leaves lanceolate, 2–8 cm long, 0.7–1.5 cm wide, irregularly pinnatifid, the lobes linear-oblong to linear, sparsely to densely strigillose, the hairs evenly distributed, rarely more dense along veins and margins, sometimes also sparsely hirsute, these hairs 0.6–1.5 mm long and confined to veins and margins; rosette leaves oblanceolate, 2–6 mm long, 1–1.5 cm wide, less divided than the stem leaves, dentate, or pinnately lobed or with oblong lobes, usually deciduous before flowering; petioles on all leaves 0–1.5 cm long. Buds erect, oblong-lanceolate, with free sepal tips 1–6 mm long. Flowers one rarely more per stem opening per day near sunset. Ovary 11–16(–18) mm long, densely strigillose, sessile. Floral tube (2.6–)3.5–4.2 cm long, flaring to 3–6 mm at the mouth, densely strigillose, glabrous within. Sepals splitting along one suture and reflexed to one side as a unit at anthesis, 1.8–3.5 cm long, 2–3 mm wide, strigillose, the margins with a conspicuous purple stripe often flecked with purple spots. Petals white, fading pink, drying purple, broadly obovate to nearly orbicular, (1.5–)2–4 cm long, (1.4–)1.7–3.6 cm wide. Staminal filaments 10–17 mm long. Anthers yellow, (6–)8–11 mm long. Style (4.4–)4.7–7 cm long; stigma lobes (3–)5–6 mm long, well elevated above the anthers at anthesis. Capsules few, hard and leathery at maturity, ovoid to narrowly ovoid, (9–)13–20 mm long, 3–5 mm diam. (excluding wings), the base cuneate, sometimes somewhat twisted, abruptly constricted to a sterile beak 2–6 mm long, with free tips ca. 0.5 mm long, the valves with a median ridge, the margins of the valves with a wing 2–2.5 mm wide extending the length of the capsule, usually widest above the middle, tapering to a pedicel-like, sterile basal portion 1–4 mm long, dehiscing ca. ⅓ the capsule length. Seeds ca. 100–130(?) per capsule, clustered in several indefinite rows (apparently reduced to one row in mature capsules), narrowly ovoid, obscurely angled, light brown, ca. 1.5 mm long, ca. 0.6–0.8 mm wide, the surface glossy, obscurely reticulate, appearing finely granular, rather persistent on the placenta. Self-compatible, but outcrossing. Mitotic chromosome number, $2n = 28$.

Distribution. Locally common in clay or sandy soils of arroyo banks or sometimes open flats, *Acacia* and *Opuntia* grasslands, *Larrea* scrub, in the Chihuahuan Desert from the vicinity of F. I. Madero, southeastern Durango to Zacatecas as far north as Concepción del Oro, southwest San Luis Potosí and vicinity of Ojuelos, northern Jalisco, 1,800–2,400 m. Flowering from May to September. Figure 14.

Additional specimens examined. MEXICO. DURANGO: vic. of Durango, 24°02′N, 104°40′W, *Palmer 966* (US); 1.7 mi. NE of Francisco I. Madero on Rt. 40, NE of Durango, 24°23′N, 104°19′W, *Wagner & Solomon 4318,* pro parte (MO). JALISCO: High Plains, Km 18, SW of Ojuelos on rd. to Aguascalientes, *McVaugh 16984* (MEXU, RSA, US). SAN LUIS POTOSÍ: San Luis Potosí, 22°09′N, 100°59′W, *Barroeta s.n.* (US), *Parry & Palmer 249* (BH, BM, E, F, G, GH, MO, NY, PH, US, VT), *Rzedowski 6157* (ENCB), *Schaffner 446* (BM, G, NY, P, US); 8 km NE de Laguna Seca, near 22°17′N, 100°52′W, *Rzedowski 6325* (ENCB, MEXU, RSA); 22 mi. NE of San Luis Potosí, *Straw & Forman 1430* (GH, MEXU, RSA); without further locality, 1891, *Nirlen s.n.* (P). ZACATECAS: 23 mi. S of Concepción del Oro along Hwy. 54, *Henrickson 6243* (MO), *Wagner & Brown 3980* (MO); 6 mi. WSW of Sierra Vieja, *Taylor 5867* (NY); 0.9 mi. E of jct. Rt. 54 on Rt. 45, E of Zacatecas, *Wagner & Solomon 4217* (MO); 7.4 mi. E of Guadalupe on Rt. 45–49, *Wagner & Solomon 4224* (MO); 7.5 mi. N of jct. Hwy. 45–49 on Hwy. 45, *Wagner & Solomon 4237* (MO); 8 mi. W of rd. to Sambrerete on Hwy. 45, *Wagner & Solomon 4251* (MO); without further locality, *Schueé s.n.* (RSA); Faral, *Schumann 531* (BM, F, GH, US).

3. Oenothera canescens Torrey & Frém. in Frém., Rep. Exped. Rocky Mts. 315. 1845. TYPE: Probably Colorado. Weld Co. or Wyoming, Morgan Co., along the South Platte River, "Upper waters of the Platte," 1–4 July 1843, *Fremont s.n.* (holotype, NY, photo MO; isotype, GH). Locality and date reconstructed with aid of McKelvey (1955: 845, 848). *Megapterium canescens* (Torrey & Frém.) Britton, Mem. Torrey Bot. Club 5: 235. 1894. *Gauropsis canescens* (Torrey & Frém.) Cockerell, Bot. Gaz. (Crawfordsville) 30: 351. 1900, nom. illeg. *Gaurella canescens* (Torrey & Frém.) A. Nels., Bot. Gaz. (Crawfordsville) 47: 437. 19 June 1909; in Coult. & A. Nels., New Man. Bot. Cent. Rocky Mts. 341. 22 Dec. 1909.

Oenothera guttulata Geyer ex Hook., London J. Bot. 6: 222. 1847. TYPE: Western Nebraska or southeastern Wyoming, perhaps Goshen Co.: (the only Wyoming county where *O. canescens* has been collected), "Plains of the upper Platte River," June 1843, *Geyer 178* (holotype, K not seen; isotypes, BM, photo MO, G). Locality reconstructed with aid of McKelvey (1955: 777). *Gaurella guttulata* (Geyer ex Hook.) Small, Bull. Torrey Bot. Club 23: 183. 1896, nom. illeg. *Gauropsis guttulata* (Geyer ex Hook.) Cockerell, Bot. Gaz. (Crawfordsville) 30: 351. 1900, nom. illeg.

Low, bushy perennial herbs with a subterranean to superficial caudex, forming clumps 10–50 cm across by adventitious shoots from lateral roots, densely strigillose throughout, the hairs (0.1–)0.4–0.6(–0.8) mm long, the stems many-branched from the base, decumbent to ascending, (10–)15–25(–38) cm long. Leaves canescent, lanceolate to linear, especially the smaller leaves, (3–)6–15(–25) mm long, (0.5–)1.5–4(–6) mm wide, sinuate-denticulate to subentire, acute at the apex, cuneate at the base in the broader leaves, subsessile. Buds erect, lance-elliptic to lanceolate in outline, the apex long-acuminate, without free tips or rarely with free tips 0.2–0.3 mm long. Flowers many opening per day near sunset. Ovary canescent, 5–10 mm long, sessile. Floral tube (8–)10–15(–17) mm long, flaring to ca. 2 mm at the mouth, glabrous within. Sepals splitting along one suture and reflexed to one side as a unit at anthesis, sometimes reflexed in pairs, (7–)8–12 mm long, (1.3–)1.5–2.2 mm wide, canescent, the margins with a reddish purple stripe, sometimes flecked with reddish purple splotches especially toward the base. Petals pink, rarely white, streaked or flecked with red, fading bright purple, obovate, (6.8–)1–1.7 cm long, (0.5–)0.6–1(–1.2) cm wide. Staminal filaments pale yellow, 6–8 mm long. Anthers yellow, often with a red longitudinal stripe, 3–6 mm long. Style (16–)22–27 mm long; stigma lobes 1.5–3(–4) mm long, well elevated above the anthers at anthesis. Capsule ovoid, (7–)9–12(–14) mm long, 2–4 mm diam. (excluding wings), the base cuneate to truncate and slightly asymmetrical, abruptly constricted to a conspicuous sterile beak (2–)3–4.5 mm long, becoming very hard at maturity, the margins of the valves with a narrow wing 0.8–1.5 mm wide, indehiscent. Seeds ca. 50–100 per capsule arranged in 2–4 irregular rows per locule, asymmetrically cuneiform or oblanceoloid (probably resulting from compression from adjacent seeds during development), angled, light brown to brown with dark spots at the distal end and at the micropyle, 1.2–1.5 mm long, 0.4–0.5 mm wide, the surface glossy, obscurely reticulate, appearing finely granular. Self-compatible, but outcrossing. Gametic chromosome number, $n = 7$.

Distribution. Locally common in prairie depressions, playas, margins of ditches, and other places with temporary water in the High Plains region from Goshen Co., Wyoming, southeast to Hayes Co., Nebraska, south through eastern Colorado, the eastern tier of counties in New Mexico, western Kansas, and to Garza and Dawson Cos. in the Texas Panhandle; also disjunct populations from Stafford, Sedgwick, and Chautauqua Cos., Kansas, (430–)750–1,700 m. Flowering from May to July, then sporadically through September. Figure 14.

Representative specimens examined. UNITED STATES. COLORADO: Cheyenne Co., 1 mi. E of Kit Carson on Hwy. 40, *Wagner 3691* (MO); Elbert Co., 15 mi. SW of Limon, *Ownbey 1303* (COLO, DS, GH, MO, MONT, NY, RM, UC, UTC, WS); Kiowa Co., 0.75 mi. W of Brandom, *Stephens & Brooks 22705* (DS, KANU); Kit Carson Co., Burlington, *Lemaire 1950* (NEB); Logan Co., 0.5 mi. E of Fleming, *Stephens 55793* (KANU); Lincoln Co., 10 mi. S of Arriba, *Christ 1436* (COLO, CS); Sedgwick Co., 17 mi. S & 3 mi. W of Julesburg, *Stephens 55690* (KANU); Washington Co., 4 mi. N & 15 mi. E of Elba, *Stephens 56128* (KANU, NY); Weld Co., 10 mi. SE of Grover, *Dodds 2125* (COLO, RM). KANSAS: Chautauqua Co., without further locality, 1897, *Hitchcock s.n.* (KSC); Cheyenne Co., 1.5 mi. S of Wheeler, *Stephens 86423* (KANU); Clark Co., 13 mi. W, 4 mi. N & 1 mi. E of Ashland, SW corner of Little Basin, *Stephens 84344* (KANU); Ellis Co., without further locality, *Smyth 2598* (KSC); Finney Co., Buffalo Wallows, *Hitchcock 162* (KSC, MO, NMC, NY, P, RM, US, YU); Gray Co., 2.5 mi. NE of Montezuma, *Stephens 54122* (KANU, NDA, NY); Greely Co., Tribune, 1892, *Reed s.n.* (KSC, UC); Hamilton Co., Syracuse, *Thompson 143* (KSC, MO, US); Kearney Co., near Lakin, 1928, *Howe s.n.* (NEB); Lane Co., 0.5 mi. W & 2.5 mi. S of Amy, *Stephens 55002* (KANU); Lincoln Co., without further locality, 1902, *Bergman s.n.* (NDA); Meade Co., 5 mi. E of Meade, *Horr 3375* (KANU); Norton Co., without further locality, 1892, *Smyth s.n.* (KSC); Scott Co., Scott City, 1900, *Granger s.n.* (NY); Sedgwick Co., Wichita, 1912, *Agrelius & Agrelius s.n.* (KANU); Seward Co., Liberal, 1892, *Carleton s.n.* (ILL, KSC); Sheridan Co., without further locality, 1931, *Weber s.n.* (KSC); Sherman Co., Goodland, 1892, *Smyth s.n.* (KSC, NY, UMO); Stafford Co., without further locality, 1885, *Kellerman s.n.* (F, MICH, MIN, MO, NY, OS, UMO, US); Stevens Co., golf course at Hugoton, *Shildneck C-4109* (ILLS); Wichita Co., 11.5 mi. S of Leoti, *Stephens 54946* (KANU). NEBRASKA: Banner Co., 20 mi. N of Kimball, *Porter & Porter 8751* (DS, GH, MIN, MSC, RM, RSA, TEX, UC); Chase Co., near Lamar, *Tolstead 411253* (ISC, MO, NEB); Cheyenne Co., Cheyenne, 1904, *Fawcett s.n.* (NEB); Deuel Co., 13

mi. E of Chappell, *Stephens 45578* (KANU, NCU); Hayes Co., 20 mi. W of Hayes Center, *Tolstead 411254* (ISC, MO, NEB, UC); Kimball Co., 9 mi. S of Kimball, *Stephens 44043* (KANU, NDA); Perkins Co., near Grant, *Tolstead 411255* (NEB). NEW MEXICO: Curry Co., Clovis, *Reynolds 252* (NEB); Quay Co., Bard, 1942, *Bradford s.n.* (NMC); Roosevelt Co., 10.5 mi. E of Elida, *Stephens 80144* (KANU); San Miguel Co., M. E. O'Connor Trust Ranch, Comic Strip Pasture, 1.8 mi. S of Rt. 104, 15 mi. E of Las Vegas, *Hill & Levandoski 12365* (MARY, MO); Union Co., 4 mi. NE of Folsom, 1951, *Clark s.n.* (UNM). OKLAHOMA: Beaver Co., 12.5 mi. W of Forgan, *Stratton 1338* (OKL, OKLA); Texas Co., Hitchland Playa near Hitchland, 1949, *Penfound s.n.* (OKLA). TEXAS: Armstrong Co., 8.75 mi. N of Paloduro, *Cory 13464* (ARIZ, POM); Bailey Co., 8 mi. NW of Baileyboro, *Rosson 844* (SAT, TTC, WTS); Briscoe Co., 1.2 mi. E of Silverton, *Whitehouse 9991* (SMU); Carson Co., 5 mi. N of Panhandle, *Shinners 8109* (SMU); Castro Co., lake S of Dimmitt, *York & Rodgers 425* (OKLA, SMU, TEX); Cochran Co., 22 mi. S of Muleshoe, Muleshoe Wildlife Refuge, *Stephens 80202* (KANU); Crosby Co., jct. of farm rds. 40 & 651, 7 mi. S of Crosbyton, 1968, *Morris s.n.* (NY); Dawson Co., on U.S. Hwy. 180, ca. 10.5 mi. E of Lamesa, *Lundell & Lundell 16972* (LL); Deaf Smith Co., 15 mi. N & 15 mi. W of Hereford, *Waller 964* (SMU, TTC); Dickens Co., 2 mi. S of McAdoo, 1965, *Rowell s.n.* (GH, KSC, OKLA, TTC, UC); Floyd Co., 1 mi. N of South Plains, *Spence 39* (DS); Garza Co., 11.1 air mi. NW of Post, *Hutchins 679* (OKLA, SMU, TTC); Gray Co., 16 mi. S of Pampa, *Stephens 76343* (KANU, NCU); Hale Co., SW of Kress, 6.6 mi. S on Hwy. 87 & 4.1 mi. W, *Whitehouse 9932* (MICH, NY, SMU, UC, US); Hall Co., 1 mi. W of Turkey, *Stephens 72179* (KANU, NY); Hansford Co., just S of Hitchland, Oklahoma, *Goodman 5288* (GH, NY, OKL, TEX); Hartley Co., 8 mi. E of Hartley, *Stephens 82120* (KANU); Hockley Co., Levelland, *Blassiugame 3932* (SAT); Hutchinson Co., 18 mi. NE of Stinnett, *Stephens 81921* (KANU); Lamb Co., 0.5 mi. S of Amherst, *Stephens 75973* (KANU, MASS, NCU); Lubbock Co., 5 mi. N of Slaton, *Rowell 8573* (GH, OKL, OKLA); Lipscomb Co., Booker on Hwy. 117, *Wallis 5048* (ARIZ, GH, OKLA, SMU); Lynn Co., Tahoka, *Tharp 4442* (TEX, US); Moore Co., 1.5 mi. W of Sunray, *Stephens 82015* (KANU); Ochiltree Co., 6.5 mi. SE of Perryton on U.S. Hwy. 83, *Wallis 4751* (GH, OKLA, SMU); Parmer Co., W edge of Hub, *Rowell 8634* (GH, OKLA, UC); Potter Co., Amarillo, *Reverchon 3840* (CAS, F, GH, LL, MIN, MO, NY, POM, US); Randall Co., ca. 1 mi. N of Canyon, *Higgins 4356* (ASU, BRY, MICH, NY, WTS); Sherman Co., 14 mi. E, 12 mi. S & 4.5 mi. E of Stratford, *Stephens 82387* (KANU). WYOMING: Goshen Co., S of Springer Reservoir, *Luce 94* (RM).

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